

## Status of Yellowstone Cutthroat Trout in Idaho

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**Abstract.**—In this study, we electrofished 961 study sites to estimate the abundance of trout (in streams only) throughout the upper Snake River basin in Idaho (and portions of adjacent states) to determine the current status of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvierii* and other nonnative salmonids and to assess introgressive hybridization between Yellowstone cutthroat trout and rainbow trout *O. mykiss*. Yellowstone cutthroat trout were the most widely distributed species of trout, followed by brook trout *Salvelinus fontinalis*, rainbow trout and rainbow trout × Yellowstone cutthroat trout hybrids, and brown trout *Salmo trutta*. Of the 457 sites that contained Yellowstone cutthroat trout, less than half also contained nonnative salmonids and only 88 contained rainbow trout and hybrids. In the 11 geographic management units (GMUs) for which sample size permitted abundance estimates, the number of 100-mm and larger trout was estimated to be about  $2.2 \pm 1.2$  million (mean  $\pm$  confidence interval); of these, about  $1.0 \pm 0.4$  million were Yellowstone cutthroat trout. Similarly, the estimated abundance of trout smaller than 100 mm was  $2.0 \pm 1.4$  million, of which about  $1.2 \pm 0.7$  million) were Yellowstone cutthroat trout. Both estimates are almost certainly biased downward owing to methodological constraints. Yellowstone cutthroat trout were divided into approximately 70 subpopulations, but estimates could be made for only 55 subpopulations; of these, 44 and 28 subpopulations contained more than 1,000 and 2,500 Yellowstone cutthroat trout, respectively. We compared morphological assessments of purity with subsequent molecular DNA analysis from 51 of the study sites and found that levels of purity were positively correlated between methods ( $r = 0.84$ ). Based on this agreement, we classified Yellowstone cutthroat trout (based on morphological characteristics alone) as pure at 81% of the study sites within these GMUs. Our results suggest that despite the presence of nonnative threats (genetic and competitive), Yellowstone cutthroat trout remain widely distributed and appear to have healthy populations in numerous river drainages in Idaho.

Like most other native salmonids in the western United States, the Yellowstone cutthroat trout *Oncorhynchus clarkii bouvierii* has, over the past century or more, experienced substantial declines in abundance and distribution in large portions of its historical range (Varley and Gresswell 1988; Gresswell 1995; May 1996; Kruse et al. 2000; May et al. 2003). Declines have been ascribed to a number of factors, but most notably to hybridization with or displacement by nonnative trout and habitat alterations caused by water storage and diversion, grazing, mineral extraction, timber harvest, and overexploitation by anglers (Thurrow et al. 1988; Varley and Gresswell 1988; Gresswell 1995). Such widely described declines have, in part, resulted in a somewhat fragmented distribution of isolated populations and ultimately led to a petition in August 1998 to list Yellowstone cutthroat trout under the Endangered Species Act, a petition that was denied (USFWS 2001; see also USFWS 2006).

Within the last 20 years, a number of status assessments have been conducted for Yellowstone cutthroat trout (e.g., Thurrow et al. 1988, 1997; Varley and Gresswell 1988; Gresswell 1995; May 1996; Kruse et al. 2000; May et al. 2003; Meyer et al. 2003b). These assessments have been mostly qualitative in nature or have focused on the proportion of assumed historical range that is no longer occupied. None have had the capability of quantitatively estimating (with associated confidence bounds) the abundance of Yellowstone cutthroat trout within individual populations or river drainages in the upper Snake River basin (USRB). Thus, in much of its historical range, true population size, distribution, and extinction risk due to demographic or genetic concerns remain unclear for Yellowstone cutthroat trout. In this study, we attempt to fill this information gap by conducting broad-scale random sampling of fish distribution and abundance throughout the USRB where Yellowstone cutthroat trout are native. A primary study objective was to estimate overall abundance of Yellowstone cutthroat trout and nonnative trout in Idaho (and portions of adjacent states) and

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to estimate abundance within major river drainages. We also sought to identify subpopulations of Yellowstone cutthroat trout within major river drainages and estimate trout abundance within them. Because rainbow trout *O. mykiss* hybridize with Yellowstone cutthroat trout, assessment of the amount of hybridization in the USBR was also a high priority.

While estimation of population size and similar demographic parameters are probably more important than genetic issues when evaluating population persistence (Lande 1988), assessment of genetic risks stemming from small population size is also desirable. Genetic risks to small populations are related to inbreeding or declines in heterozygosity, which is a function of the census population size ( $N_{\text{census}}$ ). However, it is not the absolute number of individuals in a population that is relevant to the amount of genetic variation in the population, but rather the effective population size ( $N_e$ ; Wright 1931). The importance of  $N_e$  has led to the development and general acceptance of the "50/500" rule (Franklin 1980; Soule 1980), which states that an  $N_e$  of at least 50 is needed to avoid inbreeding depression in the short term, while at least 500 is needed to avoid serious genetic drift and maintain genetic variation in the long term.

Unfortunately,  $N_e$  is difficult to estimate, especially when relying on demographic data; however, precise estimates of this parameter for management purposes are not always crucial. Approximations can provide managers with useful information regarding the relative degree of genetic loss likely to take place and seem especially helpful in prioritizing conservation efforts across multiple populations (Harris and Allendorf 1989). Rieman and Allendorf (2001) approximated  $N_e$  by using a generalized age structure simulation model to relate  $N_e$  to adult spawning numbers under a variety of life history characteristics in bull trout *Salvelinus confluentus* (some of which closely match those of Yellowstone cutthroat trout) and suggested that the most realistic estimates of  $N_e$  were between 0.5 and 1.0 times the mean number of adults spawning annually. Previously, we developed a method of estimating the number of spawners in a population by developing models that predict the size at which Yellowstone cutthroat trout mature at any given stream location (Meyer et al. 2003a). A final study objective was to use these maturity models and the abundance and size structure data we gathered in this study to approximate Yellowstone cutthroat trout  $N_e$  within as many subpopulations as possible.

### Study Area

The Snake River flows through southern Idaho from east to west, extending 1,674 km from its headwaters in

Yellowstone National Park to its confluence with the Columbia River. The USBR is defined herein as that portion of the Snake River drainage from Shoshone Falls (a 65-m natural waterfall that has isolated Yellowstone cutthroat trout from other native trout in the Columbia River basin) upstream to the headwaters of all tributaries, except the South Fork of the Snake River drainage above its confluence with the Salt River at the Idaho–Wyoming border (Figure 1). Stream surveys were conducted mostly in Idaho but also occurred within the state boundaries of Nevada, Utah, and Wyoming, where portions of the headwaters of river drainages lay outside the state of Idaho. Snowmelt heavily influences discharge in most of the 27,229 km of stream in this portion of the USBR, and discharge peaks between April and June. However, streamflow in the Snake River and in a number of major tributaries is highly regulated for agricultural and hydroelectric uses by dams and diversions. Elevation within the basin ranges from over 4,000 m at mountain peaks to 760 m at Shoshone Falls. The climate is semiarid and is characterized by an average precipitation of about 25 cm.

The historical range of Yellowstone cutthroat trout in Idaho included the entire USBR, excluding the Big Lost and Little Lost rivers (Behnke 1992). Although cutthroat trout *O. clarkii* exhibiting a "fine-spotted" morphotype have been described within the study area as a separate subspecies distinct from the Yellowstone (large-spotted) form (Behnke 1992, 2002), allozyme analyses (Loudenslager and Kitchin 1979; Allendorf and Leary 1988) and mitochondrial DNA analyses (M. Novak, Utah State University, unpublished data) have indicated no genetic differences between these morphotypes. Consequently, we made no distinction between the two forms. Nonnative trout, including rainbow trout, brook trout *Salvelinus fontinalis*, and brown trout *Salmo trutta* have been introduced throughout the basin and possess widely established, self-sustaining populations.

To facilitate summary of the available information and to provide geographic focus for conservation efforts, we subdivided the USBR into 15 geographic management units (GMUs; Lentsch et al. 2000) based largely on major river drainages, which generally also characterized the presumed historical distribution, present population status, and suspected or known movement patterns of Yellowstone cutthroat trout, as well as other management considerations (Figure 1). The Shoshone–Bannock Indian Reservation overlaps several river drainages; all streams within the reservation were excluded as a separate but unsampled GMU. Henry's Lake (in the Henry's Fork Snake River GMU), Palisades Reservoir (in the

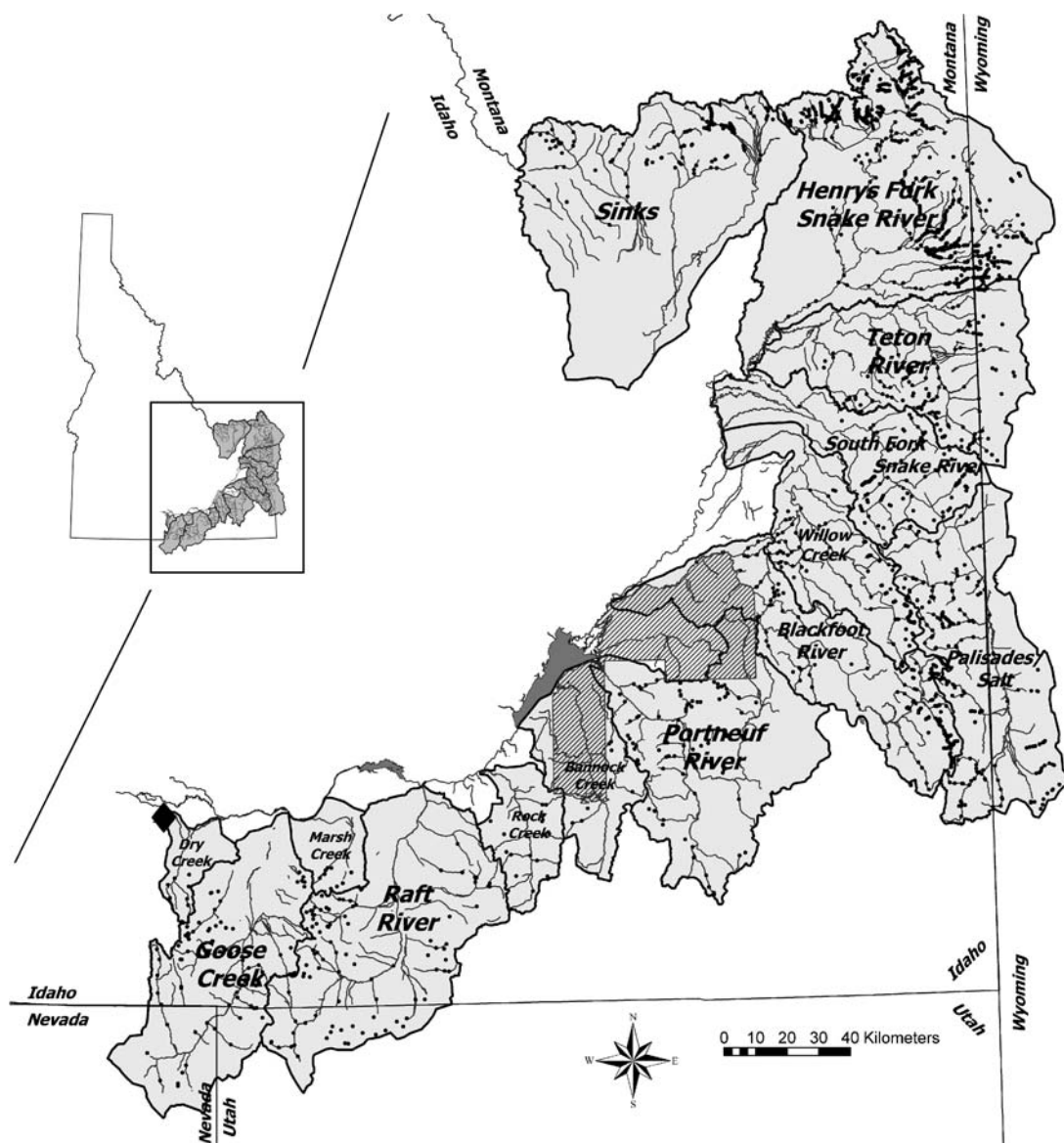


FIGURE 1.—Distribution of geographic management units (GMUs) and study sites (dots) across the upper Snake River basin in southeastern Idaho. The shaded area with diagonal hatch marks indicates the unsampled Shoshone-Bannock Indian Reservation GMU. The downstream end of the native range of Yellowstone cutthroat trout is Shoshone Falls (diamond).

Palisades-Salt River GMU), Lower and Upper Palisades lakes (in the South Fork Snake River GMU), and the main stem of the Snake River (below the confluence of the South and Henry's forks of the Snake River) contained Yellowstone cutthroat trout but were not included in our analyses because we could not obtain recent reliable abundance estimates for these bodies of water.

## Methods

### Study Site Selection

Our data collection occurred between 1999 and 2003. We selected study sites separately for each GMU with a standard 1:100,000-scale hydrography layer throughout the study. We randomly selected study streams and then randomly distributed study sites throughout each selected study stream. The density of

sites (i.e., the sample size) within a study stream and ultimately within a GMU was based on (1) time constraints, considering the vastness of the study area; (2) other recent (i.e., within the last 8 years) existing data that we used to the extent possible (16% of the sites; not necessarily distributed at random); and (3) the limited distribution of Yellowstone cutthroat trout in some GMUs, where we avoided extensive random sampling (see below).

First-order streams (see Strahler 1964) make up a large (64% at the 1:100,000 scale) portion of the stream network in the USRB, but often these headwater streams in the Rocky Mountains are either intermittent or so small that they cannot support salmonid populations (Platts 1979; Kruse et al. 1997; Dunham and Rieman 1999; Harig and Fausch 2002). In an effort to minimize confidence bounds around population estimates, sampling was proportionally reduced in first-order streams and, therefore, proportionally increased in second-order and higher streams. To accomplish this, if a first-order stream failed to become a second-order stream (but instead joined another stream that was or became second order or greater), it was not considered for sampling. This eliminated from consideration 12,850 km of the 17,795 km of first-order streams (a 72% reduction). The remaining 14,379 km of stream (all stream orders) were used for our abundance estimates. We assumed the streams that were removed contributed little to the overall abundance of trout in the USRB, and we checked this assumption by arbitrarily surveying 40 locations in these first-order streams.

When study sites occurred on private property, access was routinely obtained from landowners and was denied less than 1% of the time; roughly 26% and 74% of the sites occurred on private and public land, respectively. For our purposes, we felt the above methodology would adequately characterize the distribution and abundance of trout within GMUs while providing conservative abundance estimates, an appropriate approach when evaluating status and risk.

This methodology was modified in three GMUs: Henry's Fork Snake River, Rock Creek, and Bannock Creek, where the Yellowstone cutthroat trout distribution was too limited to accurately rely entirely on random site selection to estimate Yellowstone cutthroat trout abundance and where our goal was also to verify known or suspected Yellowstone cutthroat trout subpopulations and assess their distribution and abundance. Within this more restricted sampling framework, we distributed sites randomly so that abundance estimates could be made at the subpopulation level (see below). Using the above two sample site selection approaches across the entire study area, an

average of about one study site for every 18 km of stream (range between GMUs: one site for every 9–37 km of stream) was established.

### *Fish Sampling*

At each study site, fish were captured with electrofishing gear unless the site was dry ( $n = 239$  dry study sites). Sampling occurred during low-to-moderate flow conditions (usually late June to early October) to facilitate fish capture and to help standardize sampling conditions. Fish were identified, enumerated, measured to the nearest millimeter (total length [TL]), weighed to the nearest gram, and eventually released. The few hatchery rainbow trout (which are sterilized in Idaho) encountered were easy to differentiate from wild rainbow trout based on fin condition and were not included in this study.

Sampling in small streams (i.e., <8 m wide) was conducted by depletion electrofishing using one or more backpack electrofishers (Smith-Root, Inc., Vancouver, Washington; Model 15-D) with pulsed DC. Block nets were installed at the upper and lower ends of the sites to meet the population estimate modeling assumption that the fish populations were closed. Depletion sites were typically (69% of the time) between 80 and 120 m in length (depending on habitat types and ability to place block nets) and averaged 116 m (range = 28–2,554 m). Maximum likelihood abundance and variance estimates were calculated with the MicroFish software package (Van Deventer and Platts 1989). When all trout were captured on the first pass, we estimated abundance to be the total catch.

To increase the number of sites that could be sampled in a given amount of time, we did not make multipass depletions at all backpack electrofishing sites. Instead, using data from the multipass depletion sites ( $n = 425$  study sites), we developed (within each GMU) a linear relationship between the numbers of trout captured in first passes and maximum likelihood abundance estimates. From this relationship, we then predicted trout abundance at sites where only a single removal pass was made ( $n = 268$  study sites; Lobón-Cervia et al. 1994; Jones and Stockwell 1995; Kruse et al. 1998). Separate regression models were built for trout smaller than 100 mm TL and trout 100 mm TL or larger, and standardized residuals were investigated to remove outliers from the regression models (Montgomery 1991) before population estimates were made. Such relationships were consistently strong across all GMUs (mean  $r = 0.97$ ; range = 0.88–0.99).

At sites too large to perform backpack electrofishing ( $n = 29$ ), mark-recapture electrofishing was conducted with a canoe- or boat-mounted unit (Coffelt Mark XXII) and DC (if possible) or pulsed DC. Recapture

runs were made 2–7 d after marking fish, and we assumed that there was no movement of marked or unmarked fish into or out of the study site. Site length was much longer than for depletion sites, averaging 4,951 m (range = 332–12,000 m) and reducing the likelihood of fish movement. Log-likelihood estimates of trout abundance were made with the Mark Recapture for Windows software package (Montana Fish, Wildlife, and Parks 1997). Estimates were made for each 100-mm size-class and were summed to produce an estimate of total number of trout present. However, we could not estimate the number of trout smaller than 100 mm TL at the mark–recapture sites because of the low capture efficiencies of small fish. Abundance data at four study sites on the main-stem Salt River in Wyoming were obtained from Gelwicks et al. (2002). The estimates in that study were made only for trout 150 mm or larger; as we used their data uncorrected, we underestimated the abundance of trout 100 mm or larger at those four sites.

For all study sites, we first estimated the overall abundance of trout, then partitioned the abundance for each species by multiplying trout abundance by the proportion of the catch that each species comprised. From a Yellowstone cutthroat trout management perspective, rainbow trout and rainbow trout  $\times$  cutthroat trout hybrids (hereafter, hybrids) are alike, so they were combined for all population estimates. Because electrofishing is known to be size selective (Reynolds 1996), trout were separated into two length categories: (1) smaller than 100 mm TL and (2) 100 mm TL or larger. Abundance estimates were made separately for these two size-groups.

Our methodology resulted in a total of 961 study sites (Figure 1), which included our own fish surveys at 806 randomly selected study sites throughout the USBR plus additional data from the U.S. Forest Service (31 sites; J. Capurso, Caribou–Targhee National Forest, unpublished data), Wyoming Game and Fish Department (4 sites; Gelwicks et al. 2002), Utah Department of Natural Resources (24 sites; Thompson 2002), and University of Wyoming (96 sites; Isaak 2001).

#### *Estimation of Trout Abundance*

We estimated total trout abundance separately for each GMU using the stratified-random-sampling formulas of Scheaffer et al. (1996). We first summed the total length of stream for each stream order (or stratum; except the first-order streams that were excluded above) with ArcView geographical information systems software and divided this total by 100 m of stream (our typical study site length) to calculate the number of sampling units ( $N_i$ ) in each stratum ( $L$ ). Our

abundance estimates were also standardized to density per 100 linear meters of stream. We calculated a mean abundance ( $\bar{y}_i$ ) within each stream order (stratum) and an associated variance. For total population size ( $N_{\text{census}}$ ), we used the formula

$$N_{\text{census}} = \sum_{i=1}^L N_i \bar{y}_i,$$

and for the variance of  $N_{\text{census}}$ , we used the formula

$$\hat{V}(N_{\text{census}}) = \sum_{i=1}^L N_i^2 \left( \frac{N_i - n_i}{N_i} \right) \left( \frac{s_i^2}{n_i} \right),$$

where  $s_i^2$  is the variance of the observations in stratum  $i$  and  $n_i$  is the sample size within stratum  $i$ . All sample sites, including dry and fishless sites, were included in these estimates.

Within each GMU, we determined the number of presumably unconnected Yellowstone cutthroat trout subpopulations based on (1) our sampling and that of others, (2) personal observations and local biologists' knowledge, (3) information from a parallel study on Yellowstone cutthroat trout genetic population structure in the USBR (Cegelski et al. 2006), and (4) workshops from a separate study that were held to qualitatively assess current Yellowstone cutthroat trout status (May et al. 2003). At these workshops, current distribution (present or absent) of Yellowstone cutthroat trout was classified on a 1:100,000-scale stream hydrography layer by fisheries biologists using existing presence–absence data, professional judgment, and local expertise (see May et al. 2003 for details). Subpopulations were defined as populations that were physically disconnected from or not experiencing gene flow with other populations within the GMU. We assumed that there was no connectivity between GMUs based on genetic results cited above and on local biologists' knowledge of irrigation structures and activities and other obvious migration barriers.

We estimated individual subpopulation abundance by the same methods and formulas as above but only included stream kilometers labeled in the workshops as containing Yellowstone cutthroat trout because we believed it would more accurately represent subpopulation size and distribution. Because of small sample sizes within some stream orders, variance often could not be calculated or was unreliable for subpopulation estimates; thus, we did not calculate confidence intervals (CIs). We added abundance from all size categories into one estimate for each species. For these reasons, the estimates for subpopulations are less reliable, but we present the results for use in qualitative

assessments of the relative risks faced by individual GMUs and subpopulations within GMUs.

For the three GMUs without completely random sampling (Henry's Fork Snake River, Rock Creek, and Bannock Creek), we could not estimate trout abundance for the entire GMUs. However, we did estimate trout abundance within individual Yellowstone cutthroat trout subpopulations by following the methods described above.

*Estimation of mature Yellowstone cutthroat trout abundance and approximation of  $N_e$ .*—Using the above estimates of trout abundance, we also estimated the number of mature Yellowstone cutthroat trout by employing the established maturity modeling approach and demographic data from Meyer et al. (2003a). Logistic regression analysis was used to develop models to predict, at any given stream location, the length at which the probability of a Yellowstone cutthroat trout being mature was 0.5 (termed the maturity transition point [MTP]). Following the methods of Meyer et al. (2003a), we collected at each fish survey location four independent variables that were easy to measure and correlated to MTP: elevation ( $E$ ), width ( $W$ ), gradient ( $G$ ), and stream order ( $SO$ ). For each study site, we predicted MTP using the following logistic regression equations:

$$\text{Males : MTP}_M = (-1.2948 + 0.004E + 0.1115W - 0.795G + 1.0137SO)/0.0383$$

and

$$\text{Females : MTP}_F = (1.4368 + 0.0064E + 0.0873W - 0.9294G + 0.9145SO)/0.0581.$$

These models explained 56% and 68% of the variation (using the adjusted  $R^2$  for discrete models from Nagelkerke 1991), respectively, in the probability of maturity for 261 male and 208 female Yellowstone cutthroat trout captured across the USRB in Idaho. These models were applied to all study sites except those on the main-stem South Fork Snake River ( $n = 3$ ), for which we used the MTP values published in Meyer et al. (2003a).

For all study sites, we assumed that the sex ratio was 50:50 (see Meyer et al. 2003a) and divided Yellowstone cutthroat trout abundance by two to account for both sexes. At each study site, the actual length frequency for Yellowstone cutthroat trout was compared with the estimates of MTP at the site for both males and females to determine how many of the Yellowstone cutthroat trout present were mature. Total estimates of the number of spawning Yellowstone cutthroat trout were then extrapolated for each GMU using the same methods as above. The  $N_e$  was

approximated by assuming that values were 0.5–1.0 times the number of adult spawners (Rieman and Allendorf 2001).

*Population estimate assumptions.*—In using the above methodology, we made the following assumptions, which may have biased our estimates. First, we assumed that our electrofishing removals accurately estimated trout abundance, but we probably underestimated true fish abundance at the depletion electrofishing sites by overestimating capture efficiency, especially for trout smaller than 100 mm TL (e.g., Junge and Libosvsky 1965; Riley and Fausch 1992; Peterson et al. 2004b). Moreover, our inability to estimate density of trout smaller than 100 mm TL at our mark–recapture electrofishing sites negated our ability to include these fish in many fourth-order stream study sites and all fifth- and sixth-order sites, resulting in no additional small fish being included in estimates for these stream orders and further negatively biasing the estimates.

Second, we assumed that our 1:100,000-scale stream hydrography layer accurately represented true stream length; this assumption was probably reasonable considering that Firman and Jacobs (2002) found field-measured stream length to be, on average, only 6% longer than map-based measurements. However, a more significant source of stream layer bias was the use of the 1:100,000-scale layer instead of a 1:24,000-scale layer (unavailable at the time this study was initiated). Although streams existing on both layers are of similar length, many first-order streams that appear at the 1:24,000 scale are absent at the 1:100,000 scale. In a recent rangewide status assessment of westslope cutthroat trout *O. clarkii lewisii*, there were 35% more stream kilometers at the 1:24,000 scale than at the 1:100,000 scale (Shepard et al. 2005). Such a discrepancy results in an underestimation of trout abundance.

Third, our inclusion of nonrandom study sites may have positively biased our estimates since such sites were twice as likely to contain Yellowstone cutthroat trout as random sites. We included them in our study because they only constituted 16% of the total number of study sites. We also assumed that our one-time fish survey at each study site accurately portrayed trout abundance at the site. Although we recognize that trout abundance changes seasonally (Decker and Erman 1992) and annually (Platts and Nelson 1988; House 1995), we do not believe our study design would have directionally biased our trout abundance estimates. Considering all these potential sources of bias, we believe our design conservatively estimated trout abundance in the USRB.

### Estimation of Hybridization

The extent of Yellowstone cutthroat trout–rainbow trout hybridization was evaluated using both morphological and DNA methodologies. In the assessment of morphological characteristics, individual fish were visually classified as Yellowstone cutthroat trout, rainbow trout, or hybrids by following the protocol of Meyer et al. (2003b). To validate our morphological classification, we collected an average of 30 fin clips (range = 24–48) randomly from all *Oncorhynchus* spp. at all locations where Yellowstone cutthroat trout were encountered and where 30 fin clips could be obtained. We selected a subset of 51 study sites for DNA analyses, based largely on objectives from a companion study of Yellowstone cutthroat trout population genetic structure and genetic diversity (Cegelski et al. 2006). One diagnostic mitochondrial DNA marker, NADH dehydrogenase 2 (enzyme number 1.6.5.3; IUBMB 1992) was amplified and digested with *Rsa* I (Campbell et al. 2002). In addition, two to four diagnostic nuclear markers were also amplified and digested (if applicable) by following the polymerase chain reaction amplification, digestion, and electrophoresis protocols of Campbell et al. (2002) and Ostberg and Rodriguez (2004). The nuclear markers analyzed were *Rag3'* (Baker et al. 2002), digested with *Dde* I; *IK*, digested with *Hinf* I (Baker et al. 2002); *Occ38*; and *Occ42* (Ostberg and Rodriguez 2004). Fragments were separated by 3% agarose–Synergel electrophoresis. These markers have been used extensively to discriminate between rainbow trout and cutthroat trout (Baker et al. 2002; Ostberg and Rodriguez 2002, 2004; Baumsteiger et al. 2005) and their great utility in hybridization studies has been proven. Individual fish were classified based upon their multilocus genotypes. Individuals that scored as homozygous for the same species at all amplified markers were recorded as having genotypes indicative of either pure Yellowstone cutthroat trout or pure rainbow trout. This nomenclature was used since some later-generation hybrids can be mistaken as pure. Individuals were classified as hybrids when they exhibited alleles from both species at any locus or combination of loci, or exhibited mitochondrial DNA of one species and nuclear alleles of the other species. We compared the percentage of fish classified as pure Yellowstone cutthroat trout by morphological and molecular DNA methods with a correlation coefficient ( $n = 51$ ). We did not assess the amount of agreement at the individual level since this would require 20–30 codominant markers for an accurate genetic classification (Boecklen and Howard 1997).

We estimated the genetic percentage of introgression

for each genetic sample location as the proportion of rainbow trout alleles identified out of the total number of alleles examined. We also tested for differential introgression among loci by using a contingency table to compare genotypic frequencies of Yellowstone cutthroat trout (BB), hybrids (AB), and rainbow trout (AA). We calculated our ability to detect introgression at each of the genetic sample locations using the equation (Hitt et al. 2003)

$$A^{2n} = B,$$

where  $A$  equals 1 minus the percent introgression to be detected,  $B$  equals 1 minus the percent chance to detect that level of introgression, and  $n$  equals the genetic sample size. The genetic sample size is based on the number of individual fish analyzed and the number of diagnostic alleles examined and was reported to take into account different fin clip sample sizes and missing genotypes at some loci. At all but 4 of the 51 genetic sample locations, we had greater than a 99.9% chance of detecting as little as 3% rainbow trout introgression and a 90% chance of detecting 1% introgression. To characterize introgressive hybridization with the 10 GMUs where sites were distributed randomly (and thus where such characterization was valid), we identified those study sites containing populations that were pure or at least 90% pure, based on the multistate agreement for cutthroat trout management (UDWR 2000), which categorizes cutthroat trout into core, conservation, and sport fish populations (those with 0%, 1–10%, or >10% introgressive hybridization, respectively).

### Results

Study sites in the USRB occurred in stream reaches that were 23% first order, 43% second order, 25% third order, 6% fourth order, 2% fifth order, and 1% sixth order. Streams at the study sites ranged from 0.3 to 79 m wide (mean = 4.3 m), from 1,378 to 2,667 m in elevation (mean = 1,890 m), and from 0.01% to 19.2% in gradient (mean = 3.1%). The sample length of all study sites combined totaled 0.9% of the entire stream network (1:100,000 scale) in the USRB.

Yellowstone cutthroat trout were the most widely distributed species of trout in the USRB within the GMUs we surveyed; they were captured at 457 (48%) of the study sites (Table 1). Two hundred forty-two sites (25%) contained brook trout, 136 sites (14%) contained rainbow trout and hybrids, and 70 sites (7%) contained brown trout. Of the sites that contained Yellowstone cutthroat trout, less than half (224 of 457) contained nonnative trout. Brook trout were the most common nonnative trout found in sites with Yellowstone cutthroat trout (122 of 457 sites), followed by rainbow

TABLE 1.—Stream network and distributional extent of Yellowstone cutthroat trout (YCT), rainbow trout and hybrids (RT–HY), brook trout (BKT), and brown trout (BNT) in the upper Snake River basin (USRB) by geographic management unit (GMU), 1999–2003 (HFSR = Henry’s Fork Snake River and SFSR = South Fork Snake River).

Stream network and study site	Sinks	HFSR <sup>a</sup>	Teton	Palisades–Salt	SFSR	Willow	Blackfoot
Total kilometers in USRB	2,604	3,546	2,383	2,938	1,822	1,699	2,178
Kilometers included in trout estimates <sup>b</sup>	1,437	2,184	1,278	1,531	897	865	1,155
Total number of sites sampled	69	119	95	163	78	58	82
Sites containing trout	35	87	59	150	47	23	49
Sites containing YCT	10	34	45	148	46	21	45
Sites containing RT–HY	13	20	12	7	13	0	19
Sites containing BKT	25	72	53	22	0	4	13
Sites containing BNT	2	7	3	37	6	2	0
YCT sites containing other trout	8	27	40	56	14	4	25
YCT sites containing RT–HY	5	6	8	7	12	0	19
YCT sites containing BKT	4	24	38	21	0	2	9
YCT sites containing BNT	0	2	3	36	6	2	0
Dry or nearly dry sites	19	32	24	6	27	23	14

<sup>a</sup> GMUs where YCT distribution was restricted and where sites were not selected at random.

<sup>b</sup> Excludes the “first-order only” streams not included in our analysis (see Methods).

trout (88 sites) and brown trout (56 sites). Yellowstone cutthroat trout were captured at 328 (41%) of the 806 randomly distributed study sites, whereas they were captured at 129 (83%) of the 155 nonrandomly distributed sites. Thirty-eight percent of the study sites on private property contained Yellowstone cutthroat trout, compared with 51% of those on public property. The likelihood of trout being present was higher in higher-order streams. Trout were present in 41% of first-order streams, 64% of second-order streams, 71% of third-order streams, 76% of fourth-order streams, 83% of fifth-order streams, and 100% of sixth- and higher-order streams.

Forty arbitrarily selected sites within the 12,850 km of first-order streams that had been removed from sampling consideration were surveyed to test the assumption that they contained negligible numbers of salmonids. Twenty-four (60%) of the sites were dry. We found trout at five (13%) sites, including four that contained Yellowstone cutthroat trout. Although no formal population estimates were made at these sites, where trout were found their abundance was low (around one or fewer trout per 10 m of stream). These data were not included in any further analyses.

Estimation of Trout Abundance

For trout 100 mm TL or larger, average linear and areal densities in all GMUs combined in the USRB were 19.6 trout/100 m and 6.3 trout/100 m<sup>2</sup>, respectively (Figure 2). Mean linear density was highest in the South Fork Snake River, Palisades–Salt River, and Teton River GMUs and lowest in the Bannock Creek and Willow Creek GMUs. Mean areal density was highest in the Portneuf River, Teton River, and Raft River GMUs and lowest in the Bannock Creek and Willow Creek GMUs.

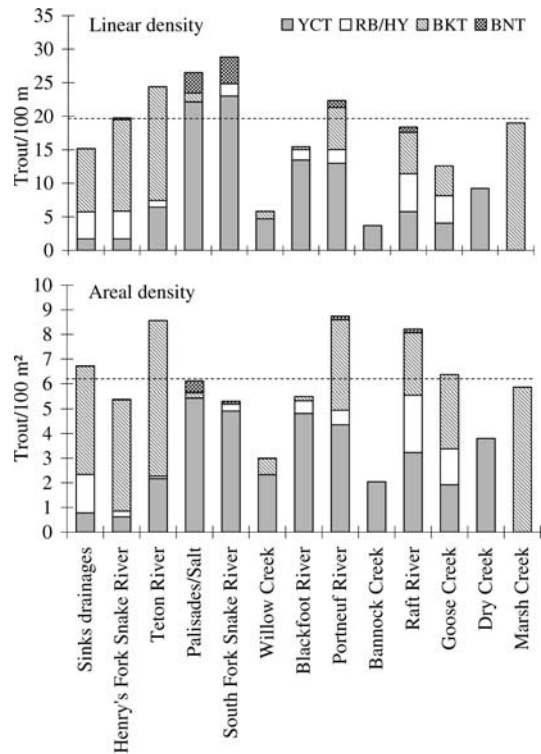


FIGURE 2.—Average linear and areal densities of Yellowstone cutthroat trout (YCT), rainbow trout and their hybrids (RB/HY), brook trout (BKT), and brown trout (BNT) from study sites in each geographic management unit in the upper Snake River basin, Idaho, 1999–2003. Dashed lines indicate the means among all study sites.



TABLE 1.—Extended.

Stream network and study site	Portneuf	Bannock <sup>a</sup>	Rock <sup>a</sup>	Raft	Goose	Dry	Marsh	Total
Total kilometers in USRB	2,225	641	650	3,769	2,446	135	437	27,229
Kilometers included in trout estimates <sup>b</sup>	1,094	257	315	1,826	1,273	75	194	14,379
Total number of sites sampled	83	7	15	95	80	7	10	961
Sites containing trout	51	3	0	53	37	3	8	605
Sites containing YCT	47	3	0	35	20	3	0	457
Sites containing RT-HY	21	0	0	17	14	0	0	136
Sites containing BKT	8	0	0	24	13	0	8	242
Sites containing BNT	7	0	0	6	0	0	0	70
YCT sites containing other trout <sup>c</sup>	25	0	0	18	7	0	0	224
YCT sites containing RT-HY	21	0	0	6	4	0	0	88
YCT sites containing BKT	4	0	0	17	3	0	0	122
YCT sites containing BNT	7	0	0	0	0	0	0	56
Dry or nearly dry sites	10	2	14	32	30	4	2	239

We estimated that there were about  $4.2 \pm 2.7$  million (mean  $\pm$  confidence interval) trout present in the 11 GMUs where trout abundance could be estimated (Table 2). Of these, about 2.2 million were Yellowstone cutthroat trout, 1.2 million were brook trout, 0.5 million were rainbow trout and hybrids, and 0.3 million were brown trout. Of the 2.2 million Yellowstone cutthroat trout estimated to be present in the study area,  $1.0 \pm 0.4$  million were estimated to be 100 mm TL or larger, and  $1.2 \pm 0.7$  million were estimated to be smaller than 100 mm TL. For trout 100 mm and larger, Yellowstone cutthroat trout made up 47% of the total abundance, followed by brook trout (27%), brown trout (13%), and rainbow trout and hybrids (13%; Table 2).

Most of the overall abundance occurred in second- and third-order streams for Yellowstone cutthroat trout (55%) and rainbow trout and hybrids (57%; Figure 3). In contrast, first- and second-order streams comprised 75% of the overall abundance for brook trout, whereas fifth- and sixth-order streams comprised 85% of the overall abundance for brown trout. Even after the removal of much of the first-order stream kilometers, first-order streams still comprised 34% of the total stream kilometers but only 18% of the total trout abundance.

Based on biologists' knowledge of Yellowstone cutthroat trout movement patterns, migration barriers, and genetic population structure, there was no evidence for separating Yellowstone cutthroat trout in the Palisades-Salt River, Willow Creek, Bannock Creek, and Dry Creek GMUs into discrete subpopulations. For the remaining seven GMUs where Yellowstone cutthroat trout existed, we estimated that there were 2–14 subpopulations within each individual GMU. Yellowstone cutthroat trout subpopulations ranged in

size from an estimated 42 fish in the Wildcat Creek subpopulation to 494,644 fish in the Palisades-Salt River population (Table 3). We estimated that of the 55 subpopulations (out of 70 total) where abundance estimates could be made, 44 (80%) contained more than 1,000 Yellowstone cutthroat trout; however, Yellowstone cutthroat trout were allopatric with other trout in only 16 (36%) of those 44 subpopulations (Table 3).

#### *Estimation of Mature Yellowstone Cutthroat Trout Abundance and Approximation of $N_e$*

We estimated that, on average, about 30% (range = 8–74%) of cutthroat trout 100 mm and larger sampled in the entire study were adult spawners. Within the 11 GMUs with abundance extrapolations, we estimated that there were about 241,000 Yellowstone cutthroat trout spawners. We estimated that  $N_e$  approximations exceeded 50 fish for 35–43 (64–78%) subpopulations and exceeded 500 fish for 10–17 (18–31%) subpopulations (Table 3).

#### *Estimation of Hybridization*

The DNA analysis identified 18 of the 51 genetic sample locations as containing rainbow trout, hybrids, or both (Table 4). Introgression levels for these populations ranged from less than 1% to 42%. The contingency test for genotypic frequencies was non-significant across the four loci ( $\chi^2 = 3.35$ ; df = 6;  $P = 0.76$ ). Therefore, there was no detectable difference in the relative contribution of each marker in its detection ability and the observed frequencies of homozygous Yellowstone cutthroat trout genotypes, hybrid genotypes, and rainbow trout genotypes at any of the four loci.

Morphological identification correctly classified the

TABLE 2.—Estimates of total trout abundance ( $N_{\text{census}}$ ) and 95% confidence intervals (CIs) for trout in 12 geographic management units (GMUs) in the upper Snake River basin, Idaho, 1999–2000. Henry’s Fork and Bannock Creek are excluded due to inadequate data.

GMU	Yellowstone cutthroat trout				Rainbow trout and hybrids			
	≥100 mm TL		<100 mm TL		≥100 mm TL		<100 mm TL	
	$N_{\text{census}}$	95% CI	$N_{\text{census}}$	95% CI	$N_{\text{census}}$	95% CI	$N_{\text{census}}$	95% CI
Sinks drainages	15,943	14,773	7,868	8,668	43,219	35,782	16,996	23,470
Teton River	85,272	26,473	120,120	80,683	22,902	24,134	1,518	908
Palisades–Salt	282,141	76,979	212,503	139,461	802	539	0	
South Fork Snake River	205,917	79,774	136,783	53,601	58,925	104,410	1,622	2,722
Willow Creek	53,509	18,632	27,526	24,820	0		0	
Blackfoot River	117,021	36,406	427,034	264,446	11,748	5,980	423	652
Portneuf River	97,961	39,312	62,460	35,420	13,577	11,773	1,639	1,402
Rock Creek <sup>a</sup>	0 <sup>b</sup>		0 <sup>b</sup>					
Raft River	101,222	35,812	100,201	55,258	91,858	55,565	163,808	177,273
Goose Creek	50,209	30,201	86,554	57,981	47,053	37,493	4,723	5,646
Dry Creek	8,770	2,390	3,425		0		0	
Marsh Creek	0		0		0		0	
Total	1,017,965	360,752	1,184,474	720,338	290,084	275,676	190,729	212,073

<sup>a</sup> GMUs where Yellowstone cutthroat trout distribution was restricted and where sites were not selected at random.

<sup>b</sup> Although no trout abundance estimates were possible, this species was absent from the GMU.

presence or absence of rainbow trout and hybrids in 43 of the 51 sites for which genetic tests were conducted (Table 4). At seven of the eight sites where morphological identification failed to correctly identify the presence of rainbow trout, hybrids, or both, rainbow trout introgression was 3% or less. The remaining site (Midnight Creek) that was incorrectly classified as pure Yellowstone cutthroat trout contained mostly (90%) juvenile fish (<100 mm), making morphological assessments difficult. The percentage of fish classified as pure Yellowstone cutthroat trout by morphological and molecular DNA methods was positively correlated ( $r = 0.84$ ;  $n = 51$ ) but biased (slope coefficient = 1.47; 95% CI = 1.20–1.74); morphological results tended to estimate higher levels of purity than did molecular DNA results (Table 4).

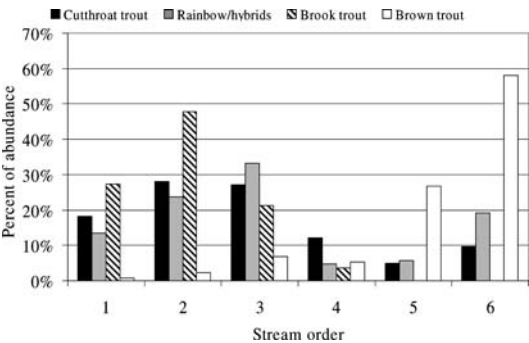


FIGURE 3.—Percent of total trout abundance (≥100 mm TL only) by stream order in the upper Snake River basin, Idaho, 1999–2003.

We assumed that the agreement we found between our morphologic characterization of hybridization and the subsequent results obtained from genetic analyses would be applicable to the remaining sites that lacked molecular information. Based on this assumption, within the 10 GMUs where Yellowstone cutthroat trout were present and abundance estimates were made, Yellowstone cutthroat trout were classified phenotypically as pure at 341 (81%) of the 420 study sites where they were found and at least 90% pure at 379 sites (90%; Table 5). Hybridization was proportionally most common in the Portneuf River (21 of 47 sites) and Blackfoot River (19 of 45 sites) GMUs, least common in the Palisades–Salt River (7 of 148 sites), Raft River (6 of 35 sites), and Teton River (8 of 45 sites) GMUs, and completely absent in the Willow Creek (0 of 21 sites) and Dry Creek (0 of 3 sites) GMUs.

Discussion

Our results indicate that the Yellowstone cutthroat trout is the most abundant and widely distributed species of trout in USRB streams. Across 12 of the 14 GMUs surveyed in Idaho, we estimate that about 2 million Yellowstone cutthroat trout are present overall; about 1 million of these are 100 mm TL or larger, and about 240,000 are mature individuals. Combined with our recent study that suggested the distribution, abundance, and size structure of Yellowstone cutthroat trout at a large number ( $n = 77$ ) of fixed stream segments in the USRB had not changed appreciably in the last 10–20 years (Meyer et al. 2003b), it appears that despite obvious declines from historical levels, Yellowstone cutthroat trout in Idaho remain relatively

TABLE 2.—Extended.

GMU	Brook trout				Brown trout			
	$\geq 100$ mm TL		$< 100$ mm TL		$\geq 100$ mm TL		$< 100$ mm TL	
	$N_{\text{census}}$	95% CI	$N_{\text{census}}$	95% CI	$N_{\text{census}}$	95% CI	$N_{\text{census}}$	95% CI
Sinks drainages	99,537	45,758	52,834	30,716	377	522	0	
Teton River	193,186	56,881	304,146	107,861	1,135	1,399	502	979
Palisades–Salt	11,906	11,161	898	1,026	70,155	27,790	11,778	16,528
South Fork Snake River	0		0		160,719	176,169	6,737	9,802
Willow Creek	9,162	14,937	27,223	50,540	2,398		640	
Blackfoot River	4,614	4,824	4,545	5,397	0		0	
Portneuf River	60,816	67,368	53,424	55,107	29,476	39,028	2,969	4,166
Rock Creek <sup>a</sup>	0 <sup>b</sup>		0 <sup>b</sup>		0 <sup>b</sup>		0 <sup>b</sup>	
Raft River	117,293	64,829	99,864	66,212	9,811	10,661	446	870
Goose Creek	57,440	53,556	75,352	86,342	0		0	
Dry Creek	0		0		0		0	
Marsh Creek	30,412	24,581	31,284	35,880	0		0	
Total	584,366	343,895	649,570	439,081	274,071	255,569	23,072	32,345

widespread and abundant. Because we did not estimate the amount of historical range occupied (see below), we cannot compare our results directly with previous status assessments. However, our results appear to concur with May et al. (2003), who estimated that Yellowstone cutthroat trout occupied about 43% of historical habitats rangewide and 61% in Idaho, a much higher occupation level than reported in some previous assessments. For example, Varley and Gresswell (1988) estimated that genetically unaltered Yellowstone cutthroat trout remained in less than 10% of their historical range and that nearly all of such fish occurred in Yellowstone National Park.

A number of sources may have biased our estimates of trout abundance. First, the use of nonrandomly selected study sites, which were over twice as likely (84% versus 40%) to have Yellowstone cutthroat trout than randomly selected sites, may have positively biased our abundance estimates, although this effect was probably small since the vast majority of sites (84%) were randomly distributed. Second, the removal of all first-order streams that themselves never became second-order streams led to a 72% reduction of the total kilometers of first-order stream in our study and may have negatively biased our trout abundance estimates. Acceptance of the assumption that these first-order streams contained minimal numbers of trout seems justified when considering that trout were found in only 13% of the sites that we spot-checked in the removed first-order streams compared with 41% of the sites in first-order streams that were not removed from our sampling frame. Nevertheless, average abundance of trout was around 1 fish/10 m of stream in the removed streams, and most of these fish were

Yellowstone cutthroat trout. Considering that we removed over 12,000 km of stream from our abundance extrapolations, it is possible that this eliminated a significant number of Yellowstone cutthroat trout from our estimates.

Another potential source of bias was our use of depletion techniques to estimate abundance, which probably underestimated true trout abundance (Junge and Libosvsky 1965; Riley and Fausch 1992; Peterson et al. 2004b). Furthermore, no estimates could be made for trout smaller than 100 mm TL at all mark–recapture sites; therefore, for more than 1,200 km of stream, no trout smaller than 100 mm TL were added to the total abundance. Use of a 1:100,000-scale stream hydrography layer instead of a 1:24,000 scale also negatively biased our trout abundance estimates (Shepard et al. 2005). Finally, two of the largest populations of Yellowstone cutthroat trout in Idaho (Henry's Lake and Palisades Reservoir) and other sizeable Yellowstone cutthroat trout populations (e.g., Lower and Upper Palisades lakes) were not included in this study because we could not obtain recent reliable abundance estimates for lentic environments. In summary, we believe that estimates for small ( $< 100$  mm TL) and large ( $\geq 100$  mm TL) trout were almost certainly lower than true abundance, both in individual subpopulations and entire GMUs. Nevertheless, the use of conservative estimates would seem highly desirable when considering their demographic implications.

Despite the apparently wide distribution of Yellowstone cutthroat trout, abundance estimates easily in excess of 2 million fish, and numerous pure or nearly pure populations, we do not deem the Yellowstone cutthroat trout in Idaho to be safe from possible further

TABLE 3.—Estimates of stream kilometers, total abundance of trout ( $N_{\text{census}}$ ), and effective population size ( $N_e$ ) within 70 individual subpopulations of Yellowstone cutthroat trout (YCT) in 14 geographic management units (GMUs) in the upper Snake River basin, Idaho, 1999–2003 (RT–HY = rainbow trout and hybrids, BKT = brook trout, BNT = brown trout). Blank spaces indicate data were inadequate to produce estimates.

GMU	Subpopulation	Total stream km	Estimates of total abundance ( $N_{\text{census}}$ ) within each YCT subpopulation				Approximate range of $N_e$
			YCT	RT–HY	BKT	BNT	
Sinks drainages	Crooked Creek	23.8					
	Fritz Creek	24.6	70	165	0	0	0
	Webber Creek	17.2	79	158	79	0	0
	Irving Creek	17.7	158	487	1,002	0	40–79
	Middle Creek						
	Indian Creek	45.9	5,012	11,240	0	0	236–472
	West Fork Rattlesnake Creek	10.8					
	East Fork Rattlesnake Creek	15.6	1,237	0	2,960	0	74–148
	Moose Creek	2.6	56	0	1,311	0	0
	Dry Creek	17.8	3,035	0	0	0	307–615
Henry’s Fork Snake River	Corral Creek	8.9					
	Henry’s Lake tributaries	21.6					
	Tygee Creek	9.8	2,388	0	0	0	13–27
	Conant Creek	26.1	1,483	69	3,183	0	39–77
	Squirrel Creek	13.8	1,925	27	2,152	0	10–19
	Boone Creek	15.5	814	0	12,982	0	11–23
	Calf Creek	7.2	2,347	0	0	0	0
	Wyoming Creek	13.6	421	269	0	0	79–158
	Robinson Creek	14.0					
	Bechler River						
Teton River	Twin Creek	8.7	185	123	740	0	0
	Moody Creek	34.3	3,184	0	22,041	112	64–128
	Packsaddle Creek	13.0	8,273	60	8,092	0	15–30
	Horseshoe Creek	19.6	4,991	37	4,806	0	35–70
	Mahogany Creek	13.3	2,931	0	6,250	0	49–98
	Badger Creek	21.5	11,128	0	0	0	203–407
	Teton Creek	31.3					
	North Leigh Creek	33.0	2,265	47	19,281	0	59–118
	South Leigh Creek						
	Darby Creek						
Palisades–Salt River	Twin Creek	10.2					
	Trail Creek and tributaries	77.0	7,048	840	19,253	0	29–59
	Teton River and tributaries	256.2	54,577	16,745	63,479	1,038	2,994–5,988
	Entire GMU	1531.0	494,644	802	12,804	81,933	20,645–41,289
South Fork Snake River	Garden Creek	11.3	1,715	0	0	0	80–159
	Fall Creek	51.7	15,202	0	0	0	297–594
	Upper Palisades Creek	30.8	23,089	19	0	0	968–1,937
	Main stem and tributaries	396.7	205,608	54,080	0	150,946	12,949–25,897
Bannock Creek	Entire GMU	17.5					
Willow Creek	Entire GMU	865.0	81,035	0	36,385	3,038	4,453–8,906
Blackfoot River	Lower river and tributaries	214.9	132,314	2,007	1,177	0	1,186–2,371
	Upper river and tributaries	262.7	134,195	6,802	2,874	0	1,073–2,145
Portneuf River	Rapid Creek	51.3	14,765	1,364	0	532	980–1,960
	Walker Creek	10.4	232	0	0	0	32–63
	Bell Marsh Creek	10.3	1,652	0	0	0	73–146
	Goodenough Creek	10.9	2,241	0	0	0	259–518
	Robbers Roost Creek	8.9	1,061	0	0	0	136–272
	Harkness Creek	9.2					
	Mink Creek	16.5	2,113	221	0	38	234–468
	Gibson Jack Creek	14.1	1,270	339	269	0	120–241
	East Bob Smith Creek	8.1	1,592	0	1,065	0	327–655
	Dempsey Creek	20.4					
Raft River	Fish Creek	11.5					
	Pebble Creek	29.8	12,749	334	0	0	589–1,178
	Toponce Creek	31.2	6,130	1,553	0	6,858	282–564
	Right Hand Fork Marsh Creek	6.6	104	0	0	0	13–26
	South Junction Creek	21.3	3,923	0	0	0	85–171
	Wildcat Creek	1.8	42	0	0	0	3–5
	Johnson Creek	13.4	3,003	0	4,890	0	49–97
	George Creek	12.6	4,971	6,093	0	0	253–506
	Onemile Creek	5.3	2,874	0	0	0	106–213
	Clear Creek	3.3	1,762	0	0	0	92–184
	Eightmile Creek	9.3	5,265	0	0	0	183–366

TABLE 3.—Continued.

GMU	Subpopulation	Total stream km	Estimates of total abundance ( $N_{\text{census}}$ ) within each YCT subpopulation				Approximate range of $N_e$
			YCT	RT-HY	BKT	BNT	
Goose Creek	Grape Creek	8.7	1,163	0	0	0	79–159
	Cassia Creek	67.8	11,182	1,432	13,051	0	375–751
	Edwards Creek	6.1	801	0	0	0	33–67
	Almo Creek	12.8	2,038	0	0	0	0
	Goose Creek	62.3	33,763	2,628	3,353	0	114–228
	Big Cottonwood Creek	35.5	20,043	263	0	0	227–454
Dry Creek	Entire GMU	75.0	12,195	0	0	0	3,239–6,477

declines in any or all of these indices. The fact that nonnative trout occurred in all but two of the smallest GMUs, outnumbered Yellowstone cutthroat trout in seven GMUs, and were present in the majority of subpopulations suggests that nonnative trout pose a clear threat to the long-term persistence of Yellowstone cutthroat trout in a number of drainages. In fact, brook trout and rainbow trout most likely pose the largest threat to the long-term persistence of individual Yellowstone cutthroat trout populations in Idaho. Yellowstone cutthroat trout could probably occupy most of the stream habitat currently occupied by other trout in the USRB if nonnative trout had not displaced them through hybridization or competition.

Brook trout were the second most common trout in the USRB, and a complete randomization of study sites in the Henry's Fork Snake River GMU would have further increased estimates of their distribution and abundance relative to other trout. Although brook trout have often been implicated in the displacement of native cutthroat trout in streams in western North America (Griffith 1988; Fausch 1989; Dunham et al. 2002), the mechanisms of displacement are incompletely understood (but see Peterson et al. 2004a). Nevertheless, the presence of brook trout in at least 25 subpopulations of Yellowstone cutthroat trout in the USRB is cause for concern. Projects to eradicate brook trout through the use of electrofishing removals have typically met with dubious results (e.g., Thompson and Rahel 1996; Meyer et al., in press; but see Shepard et al. 2002), while use of chemical treatments at the stream level are typically more successful (Finlayson et al. 2005). Our results have helped identify areas where removal of nonnative salmonids may be most beneficial and effective for Yellowstone cutthroat trout conservation.

In addition to the potential of displacement, hybridization with rainbow trout can reduce or eliminate Yellowstone cutthroat trout populations through introgressive hybridization. Based on acceptance of the assumption that usually we could visually

detect rainbow trout and hybrids with a high degree of accuracy, it appears that Yellowstone cutthroat trout–rainbow trout hybridization in the USRB, although relatively widespread, is far from ubiquitous. Indeed, at the level of individual study sites, only 19% of the 457 sites containing Yellowstone cutthroat trout also contained rainbow trout or hybrids. However, of the 55 presumed Yellowstone cutthroat trout subpopulations for which estimates could be made, at least 27 (49%) contained rainbow trout or hybrids. Such a discrepancy suggests that even within presumed subpopulations, hybridization is not always uniform (Woodruff 1973) or has not yet spread throughout some subpopulations.

We assumed that, where rainbow trout or hybrids exist, Yellowstone cutthroat trout that are present should still be designated as cutthroat trout. Recent debates on the value of hybridized populations of cutthroat trout have been fervent; opinions vary from discounting any population that is not entirely pure (Allendorf et al. 2004, 2005) to advocating preservation of populations that are up to 25% hybridized (USFWS 2003; Campton and Kaeding 2005). The Idaho Department of Fish and Game categorizes cutthroat trout into core, conservation, and sport fish populations (those with 0%, 1–10%, or >10% introgressive hybridization, respectively) and prioritizes fisheries management of such populations differently, but all are considered to have value for several reasons. First, at the scale of our existing data, it is usually difficult to know the extent of hybridization throughout an entire subpopulation. For example, Toponce Creek has an estimated 6,130 Yellowstone cutthroat trout and 1,553 rainbow trout and hybrids, but based on our limited sampling we do not know the extent to which rainbow trout genes have dispersed throughout the subpopulation. Secondly, even in Yellowstone cutthroat trout subpopulations where hybrids appear to be distributed throughout the drainage, our results suggest that hybrid swarms have not yet developed in many areas. In such areas where

TABLE 4.—Comparison of the estimated proportion of Yellowstone cutthroat trout (YCT), rainbow trout (RBT), and their hybrids (HYB) at 51 study sites in the upper Snake River basin in Idaho, 1999–2003, based on morphological and molecular DNA analyses and subsequent percent genetic introgression.

Geographic management unit	Study site	Morphological identification				Molecular DNA identification				Introgression (%)
		Fish (N)	Percent			Alleles (N)	Percent			
			YCT	RBT	HYB		YCT	RBT	HYB	
Blackfoot River	Miner Creek	71	100	0	0	182	100	0	0	0
	Lower Blackfoot River	249	96	2	2	170	97	3	0	3
	Timothy Creek	104	95	1	4	156	70	0	30	14
	Rawlins Creek	170	87	1	12	164	94	0	6	6
	Blackfoot River	213	68	15	18	94	75	0	25	10
Dry Creek	East Fork Dry Creek	30	100	0	0	174	100	0	0	0
Goose Creek	Ecklund Creek	31	100	0	0	182	100	0	0	0
Palisades–Salt River	Barnes Creek	48	100	0	0	180	100	0	0	0
	Big Elk Creek	30	100	0	0	122	100	0	0	0
	Clear Creek	42	100	0	0	244	100	0	0	0
	Crow Creek	84	100	0	0	246	100	0	0	0
	Fish Creek	168	100	0	0	248	100	0	0	0
Portneuf River	Horse Creek	80	100	0	0	248	100	0	0	0
	McCoy Creek	119	100	0	0	234	100	0	0	0
	South Fork Tincup Creek	31	100	0	0	244	100	0	0	0
	Tincup Creek	69	100	0	0	246	100	0	0	0
	Bell Marsh Creek	31	100	0	0	176	100	0	0	0
	Gibson Jack Creek	31	100	0	0	168	100	0	0	0
	Goodenough Creek	31	100	0	0	176	100	0	0	0
	Harkness Creek	31	100	0	0	248	100	0	0	0
	Inman Creek	34	100	0	0	186	100	0	0	0
	Robbers Roost Creek	31	100	0	0	246	100	0	0	0
	North Fork Rapid Creek	56	100	0	0	186	97	0	3	<1
	North Fork Pebble Creek	24	100	0	0	92	96	0	4	3
	Big Springs Creek	108	98	0	2	192	94	0	6	2
	Webb Creek	35	91	6	3	178	58	0	42	19
	Rapid Creek	80	88	0	13	190	76	3	21	17
Raft River	Middle Fork Toponce Creek	29	45	7	48	156	3	10	87	42
	Almo Creek	23	100	0	0	184	100	0	0	0
	Cottonwood Creek	39	100	0	0	172	100	0	0	0
	Eightmile Creek	20	100	0	0	80	100	0	0	0
	Green Creek	31	100	0	0	174	100	0	0	0
South Fork Snake River	New Canyon Creek	30	100	0	0	180	100	0	0	0
	Corral Canyon	29	100	0	0	174	100	0	0	0
	Garden Creek	28	100	0	0	166	100	0	0	0
	North Fork Palisades Creek	30	100	0	0	104	100	0	0	0
	North Fork Rainey Creek	31	100	0	0	182	100	0	0	0
Willow Creek	Palisades Creek	109	100	0	0	246	100	0	0	0
	Fall Creek	54	100	0	0	186	94	0	6	1
	Burns Creek	116	91	3	5	182	94	0	6	3
	Lava Creek	31	100	0	0	184	100	0	0	0
	Mill Creek	28	100	0	0	184	100	0	0	0
Teton River	Sellars Creek	31	100	0	0	224	100	0	0	0
	South Fork Sellars Creek	24	100	0	0	156	100	0	0	0
	Willow Creek	31	100	0	0	288	100	0	0	0
	North Moody Creek	34	100	0	0	176	97	0	3	<1
	Mike Harris Creek	92	100	0	0	188	97	0	3	<1
Sinks drainages	South Fork Badger Creek	74	100	0	0	176	94	0	6	1
	Teton River	229	82	12	6	226	74	13	13	6
Bannock–Rock creeks	Middle Dry Creek	66	100	0	0	184	87	0	13	3
	Midnight Creek	94	100	0	0	204	60	0	40	23

hybrid swarms have not formed and where pure Yellowstone cutthroat trout probably exist outside hybrid zones, management actions that focus on removing rainbow trout and hybrids will almost certainly reduce both the rate and spread of hybridization and introgression in these areas (e.g., Host 2003) and may actually be able to restore Yellowstone

cutthroat trout in these areas to a genetically pure or near-pure condition (Leary et al. 1995).

Although we only used two to four loci to detect rainbow trout alleles and may have missed low levels of introgressive hybridization at some sites that were deemed to contain pure Yellowstone cutthroat trout populations, we believe that this was uncommon. Our

TABLE 5.—Summary of phenotypic characterization of Yellowstone cutthroat trout (YCT) introgressive hybridization at study sites in the upper Snake River basin in Idaho within geographic management units (GMUs) where cutthroat trout were widely distributed, 1999–2003.

GMU	Sites with YCT	Sites where YCT are		Hybridization range (%)
		Pure	≥90% pure	
Sinks drainages	10	5	6	0–93
Teton River	45	37	40	0–98
Palisades–Salt River	148	142	147	0–1
South Fork Snake River	46	36	43	0–57
Willow Creek	21	21	21	
Blackfoot River	45	26	38	0–59
Portneuf River	47	26	34	0–81
Raft River	35	29	30	0–94
Goose Creek	20	16	17	0–79
Dry Creek	3	3	3	

genetic sample sizes achieved 99.9% and 90% confidence in detecting 3% and 1% introgression, respectively, at all but 4 of the 51 genetic sample locations, and of those four sites, two were identified by genetic analyses as containing hybridized individuals. Our ability to morphologically distinguish pure Yellowstone cutthroat trout from rainbow trout and hybrids concurs with the findings of Campbell et al. (2002), who also found that Yellowstone cutthroat trout could be distinguished from hybrids with a high degree of accuracy. Such distinction is more difficult with other subspecies of cutthroat trout, such as westslope cutthroat trout (Weigel et al. 2002).

Theoretically, in the absence of nonnative trout, existing or additional habitat alterations may lead to continued or even further fragmentation of subpopulations of Yellowstone cutthroat trout, but it is unlikely that either current or future fragmentation would soon threaten the actual existence of the subspecies in Idaho. However, the fact that most GMUs can be divided into several reproductively isolated populations suggests that many subpopulations of Yellowstone cutthroat trout are already facing a variety of risks inherent to their low abundance, both directional (compensation and depensation) and random (catastrophes and demographic, genetic, and environmental stochasticity) in effect. Small populations have been shown to lose adaptive genetic variation and gain maladaptive genetic variation at higher rates than larger populations (Lande 1995). However, most literature addressing population viability does not refer to species (or subspecies) of vertebrates that contain millions of individuals scattered across a large geographic area and broken into numerous populations, some of which are quite large (over 200,000 individuals).

At a smaller scale, it is difficult to resolve how many Yellowstone cutthroat trout are needed in a given subpopulation for long-term persistence and maintenance

of population-level genetic diversity, and there is no definitive standard. Applying the 50/500 rule to our results, we estimated that of the 55 subpopulations where abundance estimates could be made, 34–41 Yellowstone cutthroat trout subpopulations did not meet the 500 rule and 8–16 subpopulations did not meet the 50 rule. Despite the fact that these results are based on abundance estimates that are almost certainly quite conservative (i.e., biased low), it does appear that some of the smallest populations may already be at risk of reduced fitness through inbreeding depression and may be subject to loss of genetic diversity over the long term. However, empirical evidence suggests that cutthroat trout may not exhibit such extinction risk patterns. Rieman and Dunham (2000), working at scales similar to our subpopulations, found that small, isolated populations of cutthroat trout experienced no localized extinctions, despite extreme isolation and very low densities of fish.

Regardless of how many individuals are needed to maintain genetic diversity, Lande (1988) argued that demography is likely to be more important than genetic risks in determining population viability. Thus, while the genetic results from our companion paper suggest that smaller populations have experienced some reduction in genetic diversity (Cegelski et al. 2006), we believe that such reductions are currently less important than the small size of many Yellowstone cutthroat trout subpopulations. In general, maintaining demographically viable subpopulations of Yellowstone cutthroat trout would seem to be the foremost need and should guarantee that genetic variability is maintained if reconnections or translocations from nearby pure populations are considered.

We chose not to quantify the amount of Yellowstone cutthroat trout historical range currently occupied because of the difficulty in delineating actual historical distribution. Our results suggest that for a small but

meaningful portion of streams in the USRB, historical distribution was probably limited or nonexistent, and recent anthropogenic changes did not contribute to this absence of Yellowstone cutthroat trout. For example, of the 15 study sites surveyed (on 15 different streams) in the Rock Creek GMU, 14 were completely dry. Nearly all (>90%) of these dry sites in the Rock Creek GMU lacked a streambed channel or remnant ephemeral channel. At such sites, it was obvious that even intermittent flow was lacking; these streams are now and have, for a very long time, been naturally dry (i.e., they are not real streams). Nevertheless, they appear (on all of the 1:100,000-scale stream hydrography layers in Idaho of which we are aware) as actual streams; in fact, on a stream hydrography layer, they are indistinguishable from the rest (and majority) of the dry study sites that do contain actual streambed channels and may have contained perennial streamflow in the last century or so. Because these so-called streams would be erroneously included in any assessment that included a summation of historically occupied stream kilometers, we avoided making such calculations.

### Conclusion

Despite substantial declines in distribution and abundance from historical levels, we found that Yellowstone cutthroat trout were the most widespread and numerous species of trout in the USRB within the GMUs with abundance estimates and that many Yellowstone cutthroat trout subpopulations were apparently devoid of hybridization. We also found that Yellowstone cutthroat trout were often divided into numerous small (i.e., <2,500 individuals), presumably unconnected, subpopulations. When implementing adaptive management programs for this species, managers will have to balance (1) the potentially conflicting conservation strategies of isolating subpopulations at risk of competition and introgressive hybridization from nonnative salmonids with (2) the need to connect subpopulations at demographic risk. The distribution of nonnative salmonids poses a threat to some Yellowstone cutthroat trout subpopulations and should be controlled and reduced where necessary through use of piscicides or other means where feasible. Establishing and regularly monitoring Yellowstone cutthroat trout presence and abundance at study sites in small tributaries (in addition to several already established larger-river sites) would more completely address current trends and factors influencing those trends. Further genetic screening may also be needed to characterize Yellowstone cutthroat trout hybridization in additional subpopulations, determine whether introgressive hybridization is stable or increasing, and prioritize conservation, restoration, and

translocation activities if necessary. Such management objectives and activities will help ensure that Yellowstone cutthroat trout remain widespread and abundant in the state of Idaho and continue to provide quality sportfishing opportunities.

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